Histological study of the jaw teeth in the Devonian actinopterygian †*Cheirolepis canadensis* (Whiteaves)

by

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Abstract. – †*Cheirolepis* bears two series of teeth on its jaws: one with sharp caniniform teeth and a second one with smaller teeth. The good preservation of the fossil material from Miguasha (Canada) has allowed a histological study of the various tissues of teeth and jaws. Caniniform teeth are composed of a core of orthodentine with an apical cap of acrodine. The walls of the pulp cavity show incipient folds located at the tooth base. These folds are considered a primitive type of plicidentine whose function was to reinforce the attachment of the teeth, given that this taxon is being considered as a predator. The jaws are composed of cellular bone that shows evidence of limited remodelling.

Résumé. – Étude morphologique et histologique des dents des mâchoires de l'actinoptérygien dévonien †*Cheirolepis canadensis* (Whiteaves).

†*Cheirolepis* possède deux séries de dents sur ses mâchoires : de grandes dents caniniformes et des dents plus petites. La bonne qualité de conservation des tissus fossilisés des spécimens de Miguasha (Canada) permet de décrire la structure histologique des dents et des tissus osseux de la mâchoire. Les dents sont constituées d'un cône d'orthodentine coiffé par un massif d'acrodine. Les parois de la cavité pulpaire présentent de petits plis à la base de la dent. Ces plis sont interprétés comme une forme primitive de plicidentine dont la fonction était d'améliorer la fixation des dents sur les mâchoires chez ce taxon considéré comme un prédateur. Les tissus osseux sont constitués d'os cellulaire et font l'objet, éventuellement, de remaniement.

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The Middle and Late Devonian taxon †*Cheirolepis* Agassiz, 1835 is among the oldest Actinopterygians, and one of the very few known stem-members of this clade (Pearson, 1982; Lauder and Liem, 1983; Gardiner, 1984; Janvier, 1996; Gardiner *et al*., 2005). †*Cheirolepis* was long classified among the paleoniscoids, a paraphyletic group that included the oldest known Actinopterygians (Lütken, 1871; Pearson, 1982; Gardiner, 1984; Janvier, 1996). Many of the putative earliest and basalmost Actinopterygians have either been reclassified as stem-osteichthyans or may be Stem-Sarcopterygians (Fig. 1). Thus, †*Andreolepis* appears to be a stem-osteichthyan (Janvier, 1978; Zhu *et al*., 2009), and the Late Devonian †*Mimipiscis*, formerly known as †*Mimia* (Choo, 2011) appears to be a crown-actinopterygian (Coates, 1998; Gardiner *et al*., 2005). The Early Devonian †*Dialipina* (Schultze, 1992) has also been interpreted as a stem-osteichthyan, and the Early Devonian †*Meemannia* has recently been reinterpreted as a basal sarcopterygian, although one of the latest analyses supports the basal actinopterygian status of both taxa (Giles *et al*., 2015a). Thus, the basalmost undisputed Actinopterygians are the Late Devonian †*Tegeolepis,* †*Cheirolepis,* and a few other Middle Devonian taxa (Zhu *et al*., 2006, 2009; Swartz, 2009; Giles *et al*., 2015a).

In the taxon †*Cheirolepis,* two well-known (†*C. trailli* and †*C. canadensis)* and four poorly known species are currently recognized (Arratia and Cloutier, 2004), all found in the Devonian Old Red Sandstone (408 to 360 million years old). †*C. trailli* is found in the Middle Devonian of Scotland (Agassiz, 1833-44; Traquair, 1875), whereas †*C. canadensis* occurs in the Upper Devonian (Frasnian) of Miguasha, in the province of Quebec (Whiteaves, 1881, 1889; Lehman, 1947; Pearson and Westoll, 1979; Reed, 1992; Arratia and Cloutier, 1996). Among the more poorly known species, *C. gaugeri* and *C. gracilis* occur in the Givetian of Germany and

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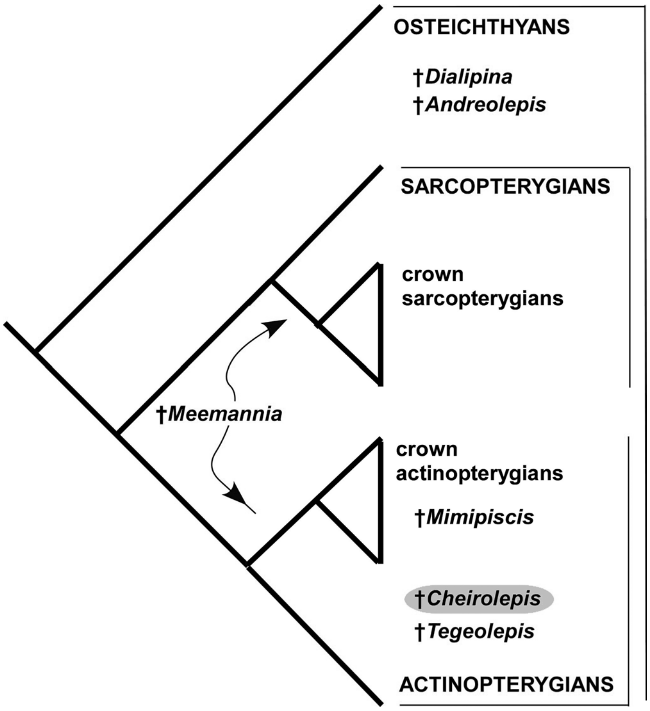

Figure 1. – Currently accepted phylogenetic position for the osteichthyans that were formerly placed in the paraphyletic "paleoniscoids".

Belarus, *C. sinualis* occurs only in Belarus, and *C. schultzei* occurs in Red Hill, dating from the Middle/Late Devonian of Nevada (Arratia and Cloutier, 2004).

†*Cheirolepis canadensis* lived in estuarine waters of the Late Devonian (Chidiac, 1996). It grew up to 50 cm in total body length, and had a highly streamlined body, which is why it is generally considered to have been capable of rapid swimming (Pearson, 1982). †*Cheirolepis canadensis* is also characterised by a heterocercal tail, a primitive feature for Actinopterygians, and also by other anatomical characters that might have favoured efficient swimming (Webb, 1978, 1980, 1984), such as the ridged surface of scales (Zylberberg *et al.*, 2016). It also bore pointed teeth in a large mouth, suggesting that it was a predator (Lehman, 1947; Arratia and Cloutier, 1996) that probably pursued its prey. The teeth probably played important functions at least in catching prey, as in various extant ichthyophagous teleosteans, for example the pike (Webb and Skadsen, 1980; Rand and Lauder, 1981; Harper and Blake, 1990, 1991; Frith and Blake, 1995). The morphology of †*Cheirolepis* teeth is relatively well-informed (Lehman, 1947; Reed, 1992; Arratia and Cloutier, 1996). Conversely, to our knowledge their histological structure is unknown. The aim of the present study is to describe the marginal teeth of *Cheirolepis* and their supporting bone at the microanatomical and histological levels. Recent studies have shown the quality of fossil material from Miguasha for paleohistological studies with *Eusthenopteron* (Zylberberg *et al.*, 2010; Meunier and Laurin, 2012). The good preservation of *Cheirolepis* fossil material (see Zylberberg *et al.*, 2016) has effectively allowed a valuable microscopical study of teeth based on ground sections. This paleohistological study uses both the traditional histological thin sections and tomography.

MATERIAL AND METHODS

Material

The present study is based on morphological and histological examination of two incomplete tooth-bearing jaw fragments of †*Cheirolepis canadensis* (Whiteaves, 1881): a piece of a right dermo-splenial preserved in external view in the sediment (MHNM 05-340) (Fig. 2A) and a fragment (MHNM 05-375A) that probably represents a maxilla (see Lehman, 1947: Pl. 3). Both specimens are hosted in the Musée d'Histoire naturelle de Miguasha (Québec, Canada). It is difficult to estimate precisely the body size from such incomplete material, but both specimens must have been about 20 cm long, judging by the relative dimensions of the preserved fragments and comparisons with more complete material, such as a specimen figured by Lehman (1947: Pl. 3).

Methods

Ground sections. – The fossil material was embedded in polyester resin (GBS 1; Brot) and sectioned for the study of teeth. Specimen MHNM 05-340 was cut to obtain four equal-sized fragments: *a*, *b*, *c* and *d* (Fig. 2). One fragment (*b*) was sectioned transversely, and two others (*a*, *d*) longitudinally to obtain respectively axial and transverse sections of teeth. The sections were polished to a thickness of about 60-80 µm and observed under transmitted natural and polarized light with a Zeiss Axiovert 35 microscope. Pictures were taken with a digital camera Olympus Camedia C-5060.

Non-destructive X-ray tomography. – The fourth fragment (*c*; see Fig. 2A) was used for X-ray tomography. The microtomographic acquisition of data was performed at the Université de Poitiers, France, with a laboratory device, the EasyTom XL Duo developed by the company RX-solutions (Chavanod, France). Specifically, the cooled L10711 Hamamatsu transmission nanofocus X-ray source was used with a LaB6 cathod and coupled to the Varian PaxScan 2520DX detector (flat panel with amorphous silicon and a CsI conversion screen; 1920 × 1536 pixel matrix; pixel pitch of 127 µm; 16 bits of dynamic range). The entire sample was scanned with a spatial resolution of 2.8 µm. Parameters of the acquisition are 60 kV (tube voltage), 96 µA (tube current), 1439 projections, a source-to-detector distance and a source-to-object distance of 5.38707 mm and 244.154 mm, respectively. Reconstruction of the data was done with the

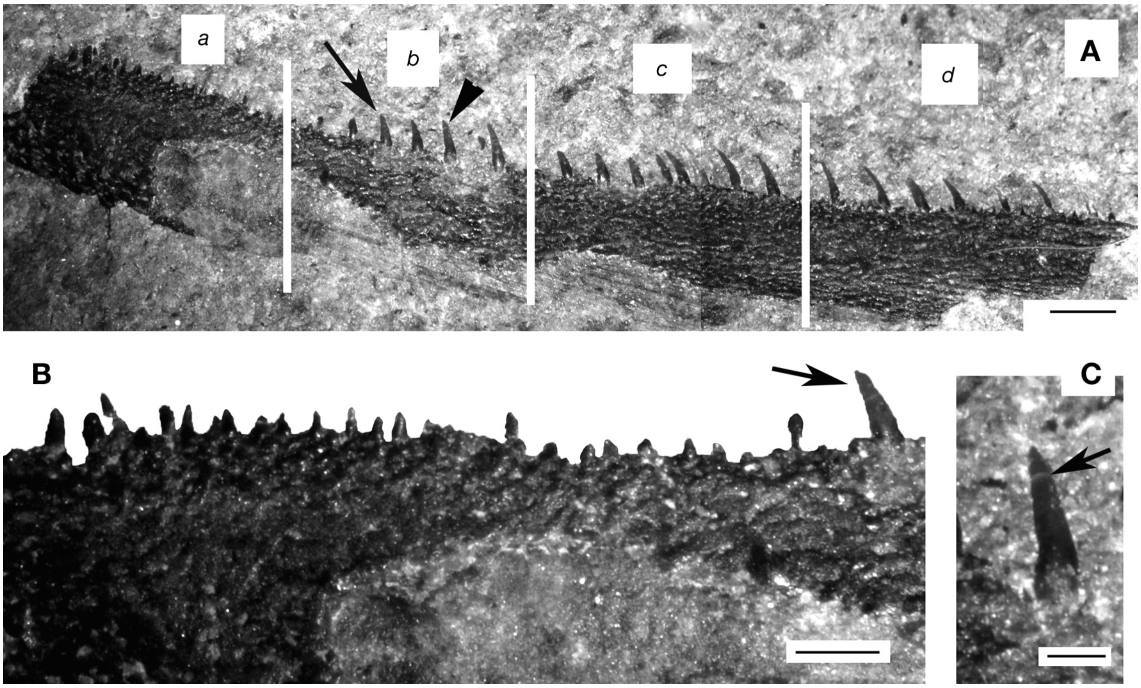

Figure 2. – Fossil material of †*Cheirolepis canadensis* (MHNM 05-340) examined in the present study. **A**: General view. The three vertical lines indicate the sections of the jaw to obtain four parts: ***a-b-c-d***. The black arrow points to the large tooth of Fig. 1B and the arrowhead to the tooth of Fig. 1C. Scale bar = 1 mm. **B**: View of the posterior part of the jaw (see fig.1A) showing the small teeth and a "fang" (arrow). Scale bar = 500 µm. **C**: External view of a large tooth showing the apical cap of acrodine (arrow). Scale bar = 250 µm.

XAct software (RX-solutions) with a classical filtered back projection algorithm and correction of the beam hardening. The segmentation of the volume reconstructed was performed with Avizo Fire 7.0.

RESULTS

Morphology of the teeth

On the surface of sample MHNM 05-340, some fine reliefs characterise the external surface of the dermo-splenial. The dermo-splenial shows two series of teeth: i) a lingual row of fairly large, sharply pointed, slightly posteriorly curved teeth (Fig. 2A); ii) a labial row of smaller teeth (Fig. 2B). The large teeth are 600/800 µm in height and 200 µm wide at their base on the jaw; the pulp cavity can be seen by transparency (Fig. 2A) and there is an apical cap of acrodine (Fig. 2C). These teeth resemble small fangs. The labial row of smaller teeth is present especially in the posterior part of the jaw (Fig. 2B), but also interspersed between the sharp teeth. These small teeth are more or less isodiametric. All teeth observed appear perfectly smooth. A tiny trace in the apical region of tooth seems to demarcate the base of a small cap of acrodine (Fig. 2C).

Histology of teeth

The longitudinal section of the subsample *a* confirms the respective location of the two series of teeth: the fangs have a lingual position, whereas the small teeth constitute a labial row (Fig. 3A). The teeth are attached to the supporting cellular bone (Fig. 3B-D).

The larger teeth are constituted of a cone of dentine around the pulp cavity. Thin canaliculi, orthogonal to the wall of the pulp cavity, penetrate deeply into the dentine core (Fig. 3F). They represent the tubular housing of cytoplasmic extensions of pulpar odontoblasts, and thus characterize orthodentine. The tooth dentine is covered by an apical cap of hypermineralized tissue (Fig. 4), that can be considered as acrodine (Ørvig, 1973, 1978a, b), which, like ganoin, appears to be a variety of enamel (Zylberberg *et al.*, 1997). At the base of the pulp cavity, dentine walls show some discrete irregular invaginations (Fig. 3D).

The histological organisation of the small teeth is similar to that of the fangs with orthodentine (Fig. 3E,G). Yet, they do not show any folding of the wall of the pulp cavity.

Histology of tooth-supporting bone and jaw bone

The jaw is composed of vascular bone (Fig. 5A, B). Star-shaped lacunae confirm the presence of osteocyte lacunae with cytoplasmic extensions that were housed in ramified canaliculi (Fig. 5C). There are no canaliculi of Williamson

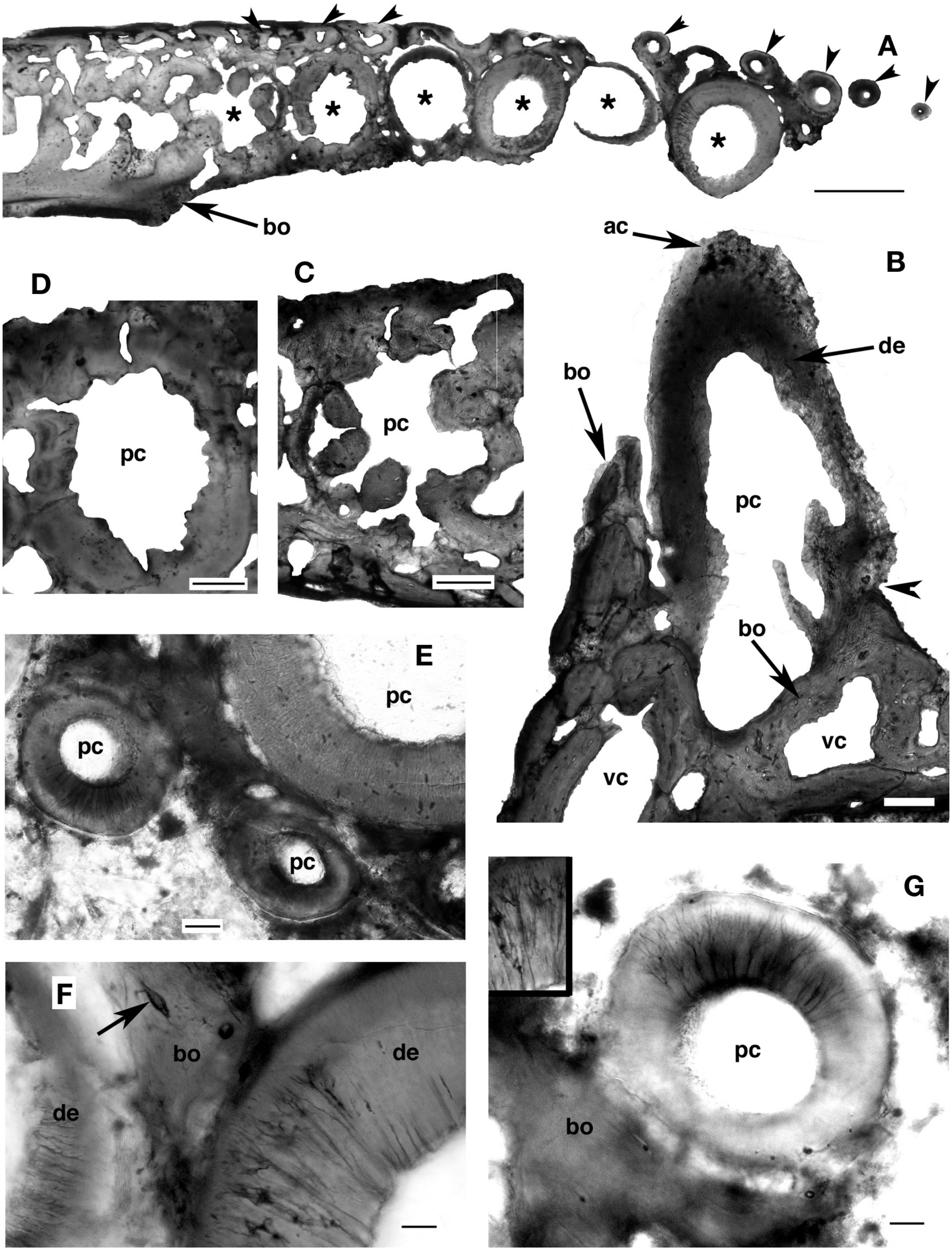

Figure 3. – Thin sections in a jaw of †*Cheirolepis canadensis* (MHNM 05-340) observed in transmitted natural light. **A**: Longitudinal ground section of fragment ***a*** (see Fig. 1A) showing the two series of teeth: the larger ones (= the fangs) (*), located lingually, and the smaller ones (arrowheads), located labially. Scale bar = 200 µm. **B**: Section of fragment ***b*** showing an axial section of a fang. The arrowhead points to the dentine ankylosed on bone. Scale bar = 50 µm. **C-D**: Two cross-sections showing details of the larger teeth at different levels. **C**: The wall of the tooth pulp cavity is crossed by vascular spaces. Scale bar = 50 µm. **D**: The walls of the pulp cavity are irregular. Scale bar = 50 µm. **E**: Detail of a large tooth and two small teeth. The section crosses the teeth halfway between their base and their tip. Scale bar = 25 µm. **F**: Detail of the contact of a tooth with the supporting bone. One can see the odontoblastic canaliculi of the orthodentine. The arrow points to an osteocyte lacuna. Scale bar = 25 µm. **G**: Cross section of a small tooth showing the odontoblastic canaliculi of the orthodentine. Scale bar = 25 µm; inset: detail of the odontoblastic canaliculi. Abbreviations: **ac** = acrodine; **bo** = bone; **de** = dentine; **pc** = pulp cavity; **vc** = vascular cavity.

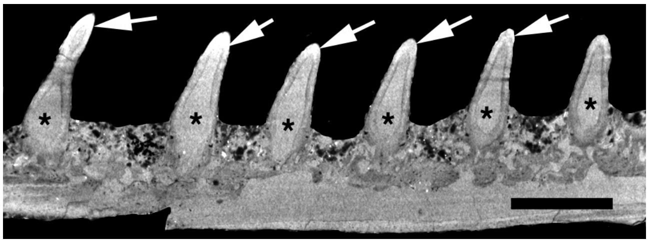

Figure 4. – Virtual section (3D-tomography) through the long axis of the jaw of †*Cheirolepis canadensis* (sub-sample ***c***; see Fig. 1A for location) showing for each tooth the dentine walls, the acrodine cap (white arrows) and the pulp cavity (*). Scale bar = 500 µm.

in the bony tissues of †*Cheirolepis*. Note that these are often called "tubules", but we prefer using the original term, proposed by Tretjakoff in 1930, for reasons explained in Meunier and Brito (2017).

Discordant bony layers can be observed here and there, especially in secondary osteons (Fig. 5B). This organization indicates that there was a remodelling process in the jaw bone, especially at the vicinity of the teeth.

3D morphology of the teeth

The virtual model of the sub-sample *c* of the jaw reveals the microanatomic features of the fangs. As already noted above, a virtual axial section of the teeth confirms the presence of a cap of acrodine (Fig. 4). Moreover, it reveals vertical folding of the dentine wall that projects into the pulp cavity, at least in its basal part, and possibly the external imprint of attachment ligaments at the tooth base (Fig. 6A, B). The fang was probably attached, through a calcified ligament to a spongy bony tissue with relatively thin trabeculae (Fig. 3A, 6B).

DISCUSSION

Our paleohistological observations further illustrate the good preservation of the studied †*Cheirolepis* material recently observed in other specimens and other vertebrate skeletal elements from the same locality (Zylberberg *et al.*, 2016). It allows a detailed histological description of teeth, their supporting jaw bone, and the cellular components of the mineralized tissues.

Bone structure

The bony tissue of †*Cheirolepis* shows typical star-shaped osteocyte lacunae with their osteocytic canaliculi and, here and there, some cementing reversal lines. Thus, †*Cheirolepis* had cellular bone (= osteocytic bone) and this confirms the paleohistological observations made on the bony tissues of their fin rays (Zylberberg *et al.*, 2016). Moreover, the bony tissue of the jaws is subject to remodelling processes. This remodelling was probably caused by vari-

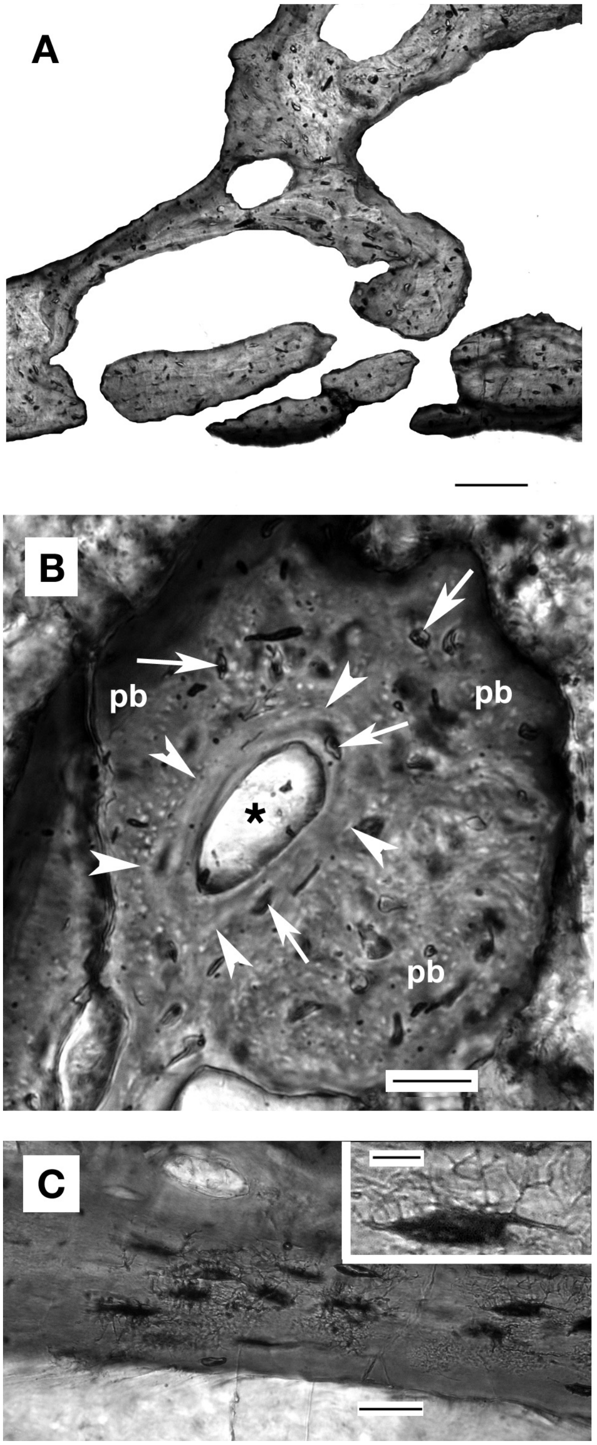

Figure 5. – Details (ground sections) of the vascularized bone in the jaw of †*Cheirolepis canadensis*. **A**. Several areas of the jaw show layers of vascularized bone with osteocyte lacunae. Scale bar = 50 µm. **B**: Detail of bony tissue with a secondary osteon (black asterisk). The white arrows point to osteocyte lacunae and arrowheads point to a cementing line between primary bone (**pb**) and the secondary osteon. Scale bar = 20 µm. **C**: Detail of bony tissue showing the spindle-shaped osteocytic lacunae. Scale bar = 25 µm. Inset: detail of an osteocyte lacuna with its ramified cytoplasmic canaliculi. Scale bar = 10 µm.

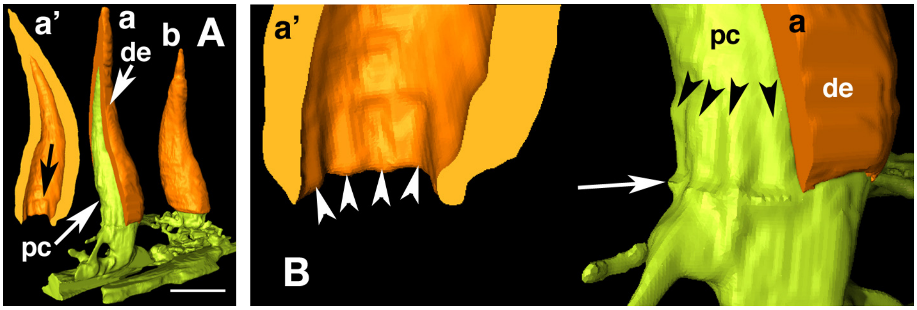

Figure 6. – Virtual reconstruction of two teeth of †*Cheirolepis canadensis* (3D-tomographic study of sub-sample ***c***; see Fig. 1A). **A**: Teeth **a** and **b** are shown in orange (**de** = dentine; the acrodine cap is not labelled separately), while green colour represents the pulp cavity and bone cavities in the supporting jaw (**pc** = pulp cavity; basal vascular canals and cavities are not labelled separately for lack of space); half of the dentine of tooth **a** (**a'**) is displaced to show the dentine folds (black arrow) and their counterpart on the wall of the pulp cavity at the base of the tooth. Scale bar = 200 µm. **B**: Detail of the base of tooth **a-a'** showing dentine folds and their counterpart (respectively white and black arrow-heads) and the print of the attachment ligament on the tooth base (white arrow).

ous factors acting in synergy: i*)* renewal of successive tooth generations, when remodelling is localized at the vicinity of the tooth bases; ii*)* remodelling constraints related to growth processes and/or to mechanical constraints during feeding; and iii*)* mineral homeostasy.

Tooth morphology

†*Cheirolepis* teeth are organized into two reasonably well-defined rows (Lehman, 1947; Reed, 1992). The larger, sharp teeth resemble small fangs. The external surface of the teeth studied in the present paper is perfectly smooth. Yet, in other specimens the external surface shows ridges. Reed (1992) noticed "a faint ridge (…) on the anterior edge of each tooth", whilst parallel axial ridges were described on the external surface of coronoid teeth (Arratia and Cloutier, 1996: fig. 14). However, those authors did not provide details of the histological characteristics of these ridged teeth.

Tooth structure

The presence of an enameloid (acrodine) covering the tooth shaft has been reported in a variety of early gnathostomes (Ørvig, 1951, 1967) and the acrodine cap is considered a synapomorphy of Actinopterygians (Patterson, 1982). Moreover, these taxa present orthodentine, which implies that the odontoblasts withdraw during dentine secretion and remain on the growing inner surface of the dental pulp (Thomasset, 1930; Lison, 1954; Ørvig, 1967; Peyer, 1968). Previously, the acrodine cap was thought to be lacking in †*Cheirolepis* (Arratia and Cloutier, 1996), which was strange given that a cap of acrodine is present on the teeth of other Actinopterygians from the Late Devonian, such as *Raynerius splendens* (Giles *et al.*, 2015b). However, our observations on †*Cheirolepis* teeth confirm the presence of an apical acrodine cap covering an orthodentine core, which represents the classical histological organisation for Actinopterygians.

Another interesting feature of †*Cheirolepis* teeth is the minute vertical folds of the dentine located at the base of the tooth in the pulp cavity. We suspect that these incipient folds represent a sort of rudimentary plicidentine organisation. Even though plicidentine has been considered for several decades as a diagnostic character of Sarcopterygians (*e.g.* Bystrow, 1939; Lison, 1954; Ørvig, 1967; Schultze, 1969, 1970), it was also described in some Actinopterygians, such as Lepisosteidae (Peyer, 1968; Schultze, 1969; Meunier and Brito, 2017) and more recently in a series of various ichthyophagous teleosts (Meunier *et al.*, 2013, 2015; Meunier, 2015; Germain *et al.*, 2016). Indeed, several studies suggest a link between the development of plicidentine and the mechanical constraints associated with a predatory diet (Peyer, 1968; Scanlon and Lee, 2002; Maxwell *et al.*, 2011; Meunier *et al.*, 2015). Folding might be a response to bite constraint, and significantly strengthen the attachment of the teeth to the jaws. †*Cheirolepis* is usually considered a predator due to its mouth morphology and rapid swimmer body shape and adaptations (*e.g.* Lehman, 1947; Arratia and Cloutier, 1996; see also introduction). †*Cheirolepis* also displays one of the oldest known cases of cannibalism among vertebrates (Arratia and Cloutier, 1996: 194). At least at Miguasha, where it was probably a top predator, it is also thought to have fed on the acanthodian *Homalacanthus concinnus* (Cloutier, 2013). Thus, the small vertical folds of the dentine pulp cavity walls constitute another evidence supporting a predatory, mainly ichthyophagous, diet for †*Cheirolepis*. The presence of plicidentine in teeth of †*Cheirolepis* shows that this spatial organization of orthodentine is very phylogenetically old, and indeed may have appeared convergently in response to strong biomechanical constraints, when the tooth attachment needed strengthening.

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